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The status of the Persian Gulf sea snake *Hydrophis lapemoides* (Gray, 1849) (Serpentes, Hydrophiidae)

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CONTENTS

SYNOPSIS. A redescription is given of the two syntypes of *Hydrophis lapemoides* together with a description of specimens from the whole range of the species. Information on breeding and feeding biology and epizooic organisms of *H. lapemoides* is provided. Geographical variation was found between the following three areas: Andaman Sea and Malacca Strait, India and Sri Lanka, and Persian Gulf and Gulf of Oman. Finally the validity of *H. lapemoides* is tested against its congeners.

INTRODUCTION

In 1849, Gray described *Hydrophis lapemoides* on the basis of two specimens from Sri Lanka and Madras, respectively. In addition to the syntypes Smith (1926) had eight specimens available for characterizing the species. Smith recorded *H. lapemoides* from the Persian Gulf, and coasts of India and Ceylon, and considered it as a rare species. Volsøe (1939) collected eight specimens in the Persian Gulf and the Gulf of Oman, and concluded that *H. lapemoides* is a fairly common snake in these waters. Minton (1966) mentioned two specimens from the coast of Pakistan, and in 1981 Toriba & Sawai extended the known range of *H. lapemoides* from the East coast of India to Penang Island, Malaysia. Tamiya et al. (1983) identified some sea snakes from the Philippines as *H. lapemoides*, the identification, however, was questioned by Rasmussen (1987). Rasmussen recorded specimens from Singapore and Phuket Island, Thailand, thereby confirming the presence of *H. lapemoides* in the Malacca Strait and Andaman Sea, respectively. Recently Gasperetti (1988) considered *H. lapemoides* as the most frequent sea snake of the Persian Gulf.

On the basis of my own collections in 1985, 1987 and 1989 from Phuket Harbour, and in 1990 from Bahrain, Persian Gulf, I have a most welcome opportunity to describe *H. lapemoides* from its whole range, and to test the validity of *H. lapemoides* against its congeners. Some comments on the biology of *H. lapemoides* are also given.

MATERIALS AND METHODS

Material examined

Hydrophis lapemoides **BMNH**: 1946.1.7.2 (syntype) (formerly III.3.3.a) Ceylon. 1946.1.6.91 (syntype) (formerly III.3.3.b) Madras. 1946.1.3.88 (type of *H. stewartii*) (formerly 83.7.30.10) Orissa, Poorie. 1946.1.9.25 (type of *H. holdsworthii*) (formerly 72.1.26.41) Ceylon. 72.1.26.43 Ceylon. 80.11.10.199 Gwadur, Baluchistan. 1904.6.13.19 Mekran coast, Charbar. 1969.2902 Persian Gulf. 1972.689 Dubai, Trucial Oman. 1971.135-136 Bahrain. 1970.753 east coast of Bahrain. 1971.1461 Bahrain harbour. 1973.410 Sharjah, Trucial coast. 1983.1169 Najwa, Darninam reef. 1983.1163-1164 Dammam channel. 1983.1170 Oqair Bay. 1983.1172 Half Moon Bay, Saudi Arabia. 1985.646 Azaiba, Batinah. **FMNH**: 28310-11 Bahrain. 64432 Tarut Bay, Ras Tonura. 73996-97 Al Khobar, Arabia. 82577 Persian Gulf 26° 39′N, 50° 07′E. 121473 Ceylon. **USNM**: 127993 Ras Tanura, Saudi Arabia. 132402 Saudi Arabia. **RMNH**: 18026 Bahrain. **ZMUC**: R 66166-173 Persian Gulf (map in Volsøe, 1939). 66101 Malacca Str. (Singapore) 1° 35′N, 103° 01′E. R 66460, 66587-603, 66605-616, 66618-627, 66629-639 all collected from trawling boats in Phuket port, Phuket Island, west coast of peninsular Thailand. R 66927, 937, 939-941, 945, 950, 951, 954, 958, 961, 964, 965, 967, 968, 970, 971, 973-975, 980-1001, 1004-1006, 1009, 1011, 1013 Persian Gulf 100 km north–northeast of Bahrain.

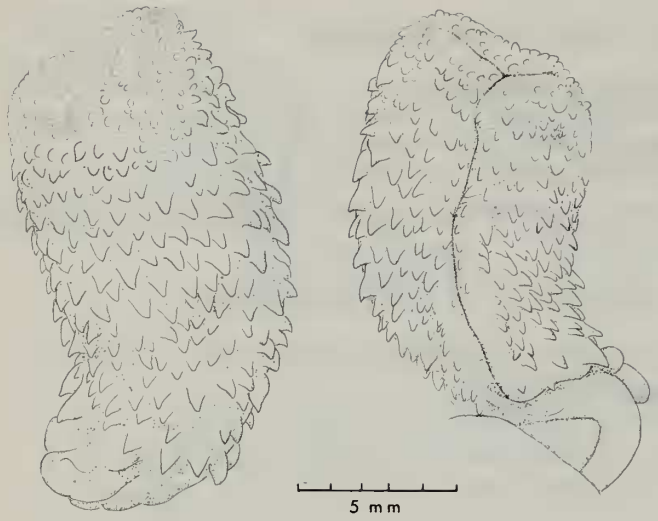

Fig. 1 Sulcate and asulcate side of everted hemipenis of *H. lapemoides* (ZMUC R 66620) from Phuket Harbour. Drawing by M. Andersen.

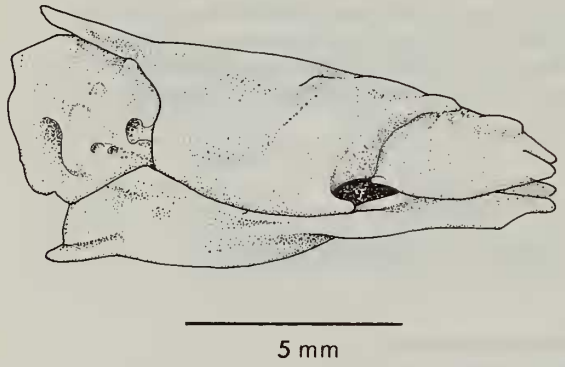

Fig. 2 Lateral aspect of anterior braincase of *H. lapemoides* in which the sphenoid is included in the margin of the anterior orifice of cavum epiptericum. Drawing by M. Andersen.

Methods

The measurements and counts follow Smith (1926) with some alterations as described below. For lateral head scales, both sides of the head have been examined and numbers are given separately. Number of maxillary teeth is given for the right side only.

Scale rows are counted directly around body (Thomas 1976). Minimum and maximum number of rows are given for comparison with the counts of Smith (1926, p.XVI).

Position of the tip of the heart and the anterior tip of the liver are determined in relation to the number of the adjacent ventral scales (VS). Relative position of the tip of the heart and the anterior part of the liver is expressed as the percentage of the total number of ventral scales (% VS). Vertebral counts are obtained from soft radiographs. Three counts are obtained from each snake: number of body vertebrae (VB-body), number of tail vertebrae (VB-tail), and number of vertebrae from the head to the tip of the heart (VB-heart). Body and tail are separated by the presence of the first pair of forked ribs in the cloacal region; this pair of ribs is included in the number of tail vertebrae. Tip of the heart was indicated in the x-ray radiographs by inserting a needle perpendicular to the long axis of the body pointing at the vertebrae opposite the tip of the heart. Relative position of the tip of the heart is expressed as the percentage of the total number of body vertebrae (% VB). Terms and description of the hemipenis follow Dowling & Savage (1960). Hemipenis was described in everted condition. All measurements are given to the nearest centimeter. Meristic and mensural data given as $x \pm SD$.

In the following description of the two syntypes *H. lapemoides* III.3.3.a, a subadult female (syntype a) is given first, and III.3.3.b, a juvenile male (syntype b) is given when different from type a. The description of the examined specimens is given in parentheses when different from the types.

The following are abbreviations (Leviton et al., 1985) used for the collections: BMNH: The Natural History Museum, London; FMNH: Field Museum of Natural History, Chicago; RMNH: Rijksmuseum van Natuurlijke Historie, Leiden; USNM: National Museum of Natural History, Smithsonian, Washington; ZMUC: Zoological Museum, University of Copenhagen.

SYSTEMATIC ACCOUNT

Hydrophis lapemoides (Gray, 1849).
Aturia lapemoides Gray, 1849:46.
Hydrophis holdsworthii Günther, 1872:33.
Hydrophis stewartii Anderson, 1872:399.
Distira lapemoides, Wall, 1909:227.
Hydrophis lapemoides, Smith, 1926:86, 1943:461. Volsøe, 1939:19. Minton, 1966:146. McDowell, 1972:229. Voris, 1977:91. De Silva, 1980:399. Toriba & Sawai, 1981:134. Rasmussen 1987:57, 1989:413, 1992:92. Gasperetti, 1988:312. Bussarawit et al. 1989:222. McCarthy & Warrell, 1991:163.

Diagnosis

Eight to 13 maxillary teeth behind poison fang, 28–35 scale rows on neck, 40–57 scale rows on body. Number of ventral scales 288–395, tip of heart extending to ventral number 106–155. Number of body vertebrae 164–188, tip of heart extending to vertebrae number 73–94. Head dark dorsally with curved white mark, disappearing with age. Body with black bands forming rhombic spots dorsally and disappearing with age ventrally. Tail with black bands, disappearing with age, posterior part normally black.

Description of the syntypes and the examined specimens

EXTERNAL MORPHOLOGICAL CHARACTERS. Maxillary teeth behind poison-fang 10. Dentary teeth, pterygoid teeth and palatine teeth not counted on syntypes; for the examined specimens see Table 1. One pre- and two postoculars on both sides (one pre- and two or three postoculars). Three anterior temporals on both sides (two or three). Eight supralabials on both sides (7-10 in males, 7-10 in females). First and second supralabials in contact with nasal, second and third in contact with preocular, third and fourth in contact with eye, syntype b; only third in contact with eye, fourth is divided horizontally. Eight infralabials on both sides, first, second and third on each side in contact with anterior pair of sublinguals,

Fig. 3 Habitus of the juvenile type specimen of *H. lapemoides* (BMNH 1946.1.6.91) from Madras, India. Photo by G. Brovad.

which are well developed and in contact with one another; third and fourth infralabials touching posterior pair of sublinguals, which are well developed and separated from one another posteriorly. A series of small cuneated scales at the oral margin after the third infralabial, syntype b; second infralabial. Scale rows on neck 29, syntype b; 32 (28-34 in males, 28-35 in females), on body 45, syntype b; 51 (40-51 in males, 41-57 in females). Ventrals 349, syntype b; 318 (288-365 in males, 293-395 in females), distinct throughout, bicarinate, about twice as broad as adjacent scales anteriorly, narrower posteriorly. Subcaudals 44, syntype b; 49 (37-56 in males, 36-53 in females).

INTERNAL MORPHOLOGICAL CHARACTERS. Tip of heart extending to ventral scale number 127, syntype b; 119 (106-141 in males, 106-155 in females), %VS heart 36.38%, syntype b; 37.42% (34.2-41.5 in males, 33.8-40.9 in females). Anterior end of liver situated at ventral scale number 133, syntype b; 120 (110-144 in males, 107-157 in females), %VS liver 38.10%, syntype b; 37.74% (34.4-41.5% in males, 34.4-41.2%). In type a, a small interval separates the heart and the liver. Number of body vertebrae 171, syntype b; 165 (164-188 in males, 171-186 in females). Number of tail vertebrae 33, syntype b; 30 (31-40 in males, 28-38 in females). Tip of heart extending to vertebrae number 81, syntype b; 82 (73-90 in males, 79-94 in females), %VB heart 47.36%, in syntype b; 49.70% (43.5-51.1% in males, 45.1-51.7% in females).

HEMIPENIS. Hemipenis feebly bilobed with a bifurcate sulcus spermaticus (Fig. 1). Bifurcation near apical end of organ (Fig. 1). Organ covered with spines gradually decreasing in size and becoming more scattered at the distal end. A finger-like fold at the proximal portion opposite the sulcus spermaticus.

SKULL MORPHOLOGY (based on skulls from the Persian Gulf and Andaman sea (Phuket)). Posterior half of parietal with a distinct ridge being about 1/3 of the total length (midline). Supratemporals (squamosals) reach parietal, and extend as far posteriorly as posterior part of exoccipitals. Postorbital bones barely touch frontals. Ventral extensions of frontals do not overhang trabecular grooves. Sphenoid enters broadly into margin of anterior orifice of cavum epiptericum (Fig. 2). Sphenoid with low but distinct keel. Both anterior and posterior Vidian foramen on the ventral side of sphenoid, and

Table 1 Geographic variation in number of the teeth on maxilla, palatine, pterygoid and dentary bone.

	n	Maxillary teeth	*n*	Palatine teeth	Pterygoid teeth	Dentary teeth
Andaman Sea Malacca Str.	53	10–13	20	8–10	23–30	20–23
India Sri Lanka	5	9–10	–	–	–	–
Persian Gulf Gulf of Oman	73	8–11	12	7–10	21–26	20–21

going back, yellowish ventrally, some older specimens without a curved mark. Body with black bands (29-52) forming rhombic spots dorsally and disappearing with age ventrally (Figs. 4 and 5). Tail with black bands (5-8), disappearing with age, posterior part black (Fig. 4).

BREEDING BIOLOGY. Six of 17 females (collected in September-November 1987) from Phuket were pregnant. Three specimens contained 2 full-term embryos each, two specimens contained 4 full-term embryos each, and one specimen contained 1 full-term embryo. Pregnant females were collected in the period 3rd October to 4th November. None of the females collected in February–March 1989 were pregnant. The smallest embryo measured 9 cm (3rd October)

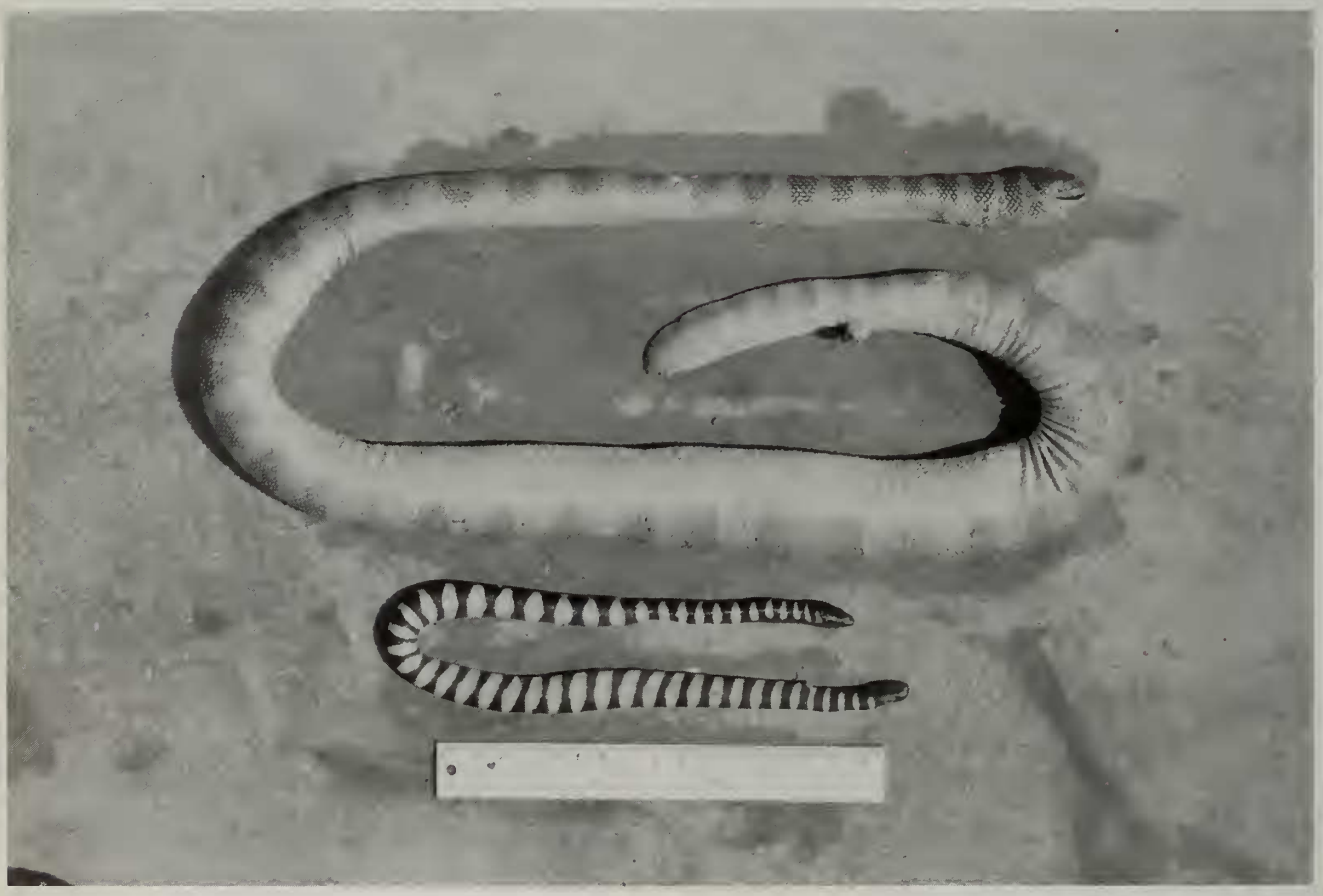

Fig. 4 Habitus of a juvenile and an adult *H. lapemoides* (ZMUC R 66992, 66993) from the Persian Gulf. Photo by M. Andersen.

in respect of the length of the Vidian canals they are symmetric. Palatine exceeding maxilla in forward extension, and without a flange for the anterior medial process of maxilla. Palatine-pterygoid articulation anterior to maxilla-ectopterygoid articulation. Fangs separated from solid maxillary teeth by a diastema. Maxillary bone slightly longer than ectopterygoid. Solid maxillary teeth shorter than fangs. For number of teeth on maxilla, palatine, pterygoid, and dentary bones see Table 1.

COLOUR. Juveniles: Head black with a yellowish curved mark above, body yellowish or whitish, encircled by black bands broadest dorsally (Figs. 3 and 4). Adults: Head dark dorsally with curved white mark above, starting forehead

and the largest 26 cm (19th October). The female collected 4th November had embryos measuring 22 cm. Thus *H. lapemoides* seems to be a k-strategist (Lemen & Voris, 1981) producing small clutches of relatively large offspring.

None of the females examined from the Persian Gulf were pregnant, however, Volsøe (1939) mentioned three females with eggs, and again the clutch size was very small (two females with 2 eggs, one female with 3 eggs). Only two of the three specimens have a collection date, and both were from April (Volsøe, 1939).

FEEDING BIOLOGY. Remains of the following four fish families were identified in stomach contents from *H. lapemoides* collected at Phuket harbour; Gobiidae, Labridae, Mullidae,

Fig. 5 Habitus of the subadult type specimen of *H. lapemoides* (BMNH 1946.1.7.2) from Sri Lanka. Photo by G. Brovad.

and Pseudochromidae. Pseudochromidae was found as prey in a sea snake stomach for the first time, and Labridae and Mullidae are new prey records for *H. lapemoides* (Voris & Voris, 1983). The stomach contents from *H. lapemoides* collected in Bahrain were too digested to be identified, however, Volsøe (1939) mentioned Gobiidae in stomachs of 5 specimens of *H. lapemoides* from the Persian Gulf. Furthermore Voris & Voris (1983) mentioned Anguilliformes and Ophicthidae as stomach contents from *H. lapemoides*.

EPIZOOIC ORGANISMS. Five of the 51 specimens examined from the Andaman Sea and Malacca Strait had between one and five barnacles (*Platylepas ophiophilus*) on the skin. Two of the seven specimens from India and Sri Lanka had three and 20 *P. ophiophilus* on the skin, respectively. 25 of the 71 specimens from the Persian Gulf and the Gulf of Oman had between one and 181 *P. ophiophilus* on the skin. Most of the barnacles were on the posterior part of the body. *P. ophiophilus* is found only on sea snakes (Zann et al., 1975), and has been found on many species (Rasmussen, 1992; Zann, 1975).

DISTRIBUTION. *H. lapemoides* is found from the Persian Gulf in west, to the Malacca Strait (Singapore) in east. Specimens have been collected from the Persian Gulf, the Gulf of Oman, the coast of Pakistan, India, and Sri Lanka, the west coast of peninsular Thailand, Penang (Malaysia), and Singapore. (Ahmed, 1975; Bussarawit et al., 1989; Gasperetti, 1988; McCarthy & Warrell, 1991; Minton, 1966; Rasmussen, 1987; Smith, 1926, 1943; Toriba & Sawai, 1981; Volsøe, 1939;).

RECENT COLLECTION DATA. *H. lapemoides* was collected in different periods of 1985, 1987, and 1989 from fishing boats in Phuket harbour, Phuket Island, on the west coast of peninsular Thailand. The most common sea snake brought to the harbour by fishing boats was *Lapemis hardwickii* (over 80% of all sea snakes caught by trawl) followed by *H. ornatus*, and then *H. lapemoides*. According to the fishermen, the sea snakes were caught mainly by sea-going trawler-boats, fishing in waters more than 10 m deep. No further information was available, as the fishermen were rather secretive about the exact position of their fishing grounds. During collection in the Persian Gulf (Bahrain) in February 1990, we went to an area about 100 km north-northeast of Bahrain, on board a trawling boat. On a 3 days trip we collected 7 specimens of *H. lapemoides*, 2 specimens of *Thalassophina viperina*, and 1 specimen of *H. ornatus*. They were all caught by trawl in a depth of 27-30 m, the bottom material was gravel. We also collected sea snakes at Bahrain harbour from 6 trawling boats, all working in the same area as mentioned above. In a period of 10 days (each boat was out 3 to 4 times in that period), a total of 110 sea snakes was collected, and 96% of the snakes were identified as *H. lapemoides*.

SPECIES ASSIGNMENT. The material examined is separated into three geographical regions: Andaman Sea and Malacca Strait, India and Sri Lanka, and Persian Gulf and Gulf of Oman (Tables 2 and 3, Figs. 6 and 7). When comparing specimens from the three areas mentioned above, geographical variation is found in general body form (specimens from the Persian Gulf look more robust than specimens from Andaman Sea and Malacca Strait), in scale rows on neck in relation to scale rows on body (Fig. 6), in number of vertebrae (Table 3), and in number of vertebrae in relation to VB heart (Table 3, Fig. 7). However, it is difficult to decide whether the variation indicates a cline or distinct geographic forms, as material is still missing from Bangladesh and Burma, and so are representative samples from Pakistan, India, and Sri Lanka.

Both Boulenger (1896), Wall (1909) and Smith (1926) referred the type specimen described by Anderson in 1872 under the name *H. stewartii* to *H. lapemoides*. Having examined the specimen, I have serious doubt about its assignment. 52 Scale rows on body in relation to 30 scale rows on neck (Fig. 6), and 182 vertebrae in relation to 94 VB heart (Fig. 7) indicate that the specimen belongs to a distinct taxon. But as representative material is lacking from India and Sri Lanka, I tentatively assign it to *H.lapemoides*. Further material may show whether it is a valid taxon.

Dunson & Minton (1978) caught some sea snakes in the Philippines, during the Visayan Sea Expedition of R/V Alpha Helix, and identified them as *H. ornatus*. In 1983 Tamiya et al. reclassified the specimens as *H. lapemoides*, and later Rasmussen (1989) reexamined the specimens and identified them as *H. lamberti*. Comparison of the above mentioned specimens with *H. lapemoides* from Andaman Sea and Malacca Strait, shows that they differ in following characters: Scale rows on neck (*H. lamberti*, 37-45), VS heart tip (*H. lamberti*, 87-109), and VS liver (*H. lamberti*, 86-108), VB heart tip (*H. lamberti*, 65-71), and color pattern (Rasmussen, 1989). Comparing the skull, *H. lamberti* shows a more robust parietal, with a longer ridge (from 1/2 to 2/3 of the total length of parietal bone in midline), and with a less globular form than *H. lapemoides*. A single specimen of *H. lamberti* (FMNH 313058) was collected sympatrically with *H. lapemoides* (ZMUC 66101) in the area of Singapore, and also here the two species are distinct on the characters mentioned above.

McCarthy & Warrell (1991) referred to a specimen (BMNH 1987.172) from the Gulf of Siam (Samut Sakhon) as '*H. sp* near *H. lapemoides*'. I have examined this specimen and agree that it is very similar to *H. lapemoides*, however, it differs in number of scale rows around body in relation to scale rows on neck (Fig. 6) and in number of vertebrae in relation to VB heart (Fig. 7). Compared to *H. lapemoides* from Malacca Strait and Andaman Sea it is very long (1.1 m) and very robust in body and head form. In general shape it is much closer to *H. ornatus* and *H. lamberti*, although the characters differ here, too. Accordingly I think '*H. sp.* near *H. lapemoides*' should be separated from *H. lapemoides*, but further studies are needed to find out whether the specimen belongs to some of the more robust species in the Gulf of Siam or is an unknown species.

Generic assignment

H. lapemoides has a combination of characters which places it in the genus *Hydrophis* as defined by Smith (1926): maxillary bone not extending forward beyond the palatine; poison-fang followed, after a diastema, by from 1 to 18 teeth; palatine straight; nostrils superior; nasal shields in contact with one another; head shields large, regular; and ventrals small, distinct throughout and normally entire.

MCDOWELL'S SUBGENERIC ASSIGNMENT. In 1972 McDowell recognized three subgenera in the genus *Hydrophis*, however, making a cladistic analysis (Rasmussen, in press) of the subgenus *Chitulia* (formerly *Aturia*, see Williams & Wallach, 1989), the results indicated that the group was paraphyletic, held together by plesiomorphic character states. Nevertheless, many of McDowell's character states are most useful in making a congeneric comparison.

Comparison with sympatric species

In the genus *Hydrophis* the following species are sympatric with *H. lapemoides*: *H. bituberculatus*, *H. brookii*, *H. caerulescens*, *H. cantoris*, *H. cyanocinctus*, *H. fasciatus*, *H. gracilis*, *H. inornatus*, *H. klossi*, *H. lamberti*, *H. mamillaris*, *H. melanosoma*, *H. obscurus*, *H. ornatus*, *H. spiralis*, *H. stricticollis*, and *H. torquatus*. (Bussarawit et al., 1989; De Silva, 1980; Gasperetti, 1988; McCarthy & Warrell, 1991; Minton, 1966; Murthy,

Table 2 Geographic variation of external and internal characters in *H.lapemoides*.

	Sex	*n*	Ventrals	VS-heart	%VS-heart	VS-liver	%VS-liver
Andaman	M	28	288–347	106–131	34.2–40.6	110–133	35.7–41.3
Sea and		*x*±SD	317±13	118±6.7	37.5±1.4	120±6.2	38.1±1.3
Malacca	F	23	299–378	106–140	33.8–38.5	107–143	34.4–39.1
Str.		*x*±SD	341±20	122±7.7	35.7±1.2	124±7.7	36.3±1.2
India	M	2	313–318	114–119	36.4–37.4	114–120	34.4–37.7
and Sri		*x*±SD	315±3.5	116±35	36.9±0.7	117±4.2	37.1±0.9
Lanka	F	5	313–376	117–145	35.1–39.0	117–146	35.1–39.3
		x±SD	347±24	127±12	37.3±1.8	129±13	37.8±1.8
Persian	M	45	293–369	111–141	35.0–41.5	113–144	36.3–41.5
Gulf and		*x*±SD	320±16	123±7.2	38.5±1.4	124±7.1	38.8±1.4
Gulf of	F	25	300–395	114–155	34.6–40.9	114–157	34.6–41.2
Oman		*x*±SD	347±23	129±10	37.5±1.6	130±10	37.7±1.6

VS-heart, VS-liver = position of tip of the heart and anterior tip of liver in relation to the number of the adjacent ventral scales, respectively. %VS-heart, %VS-liver = relative position of tip of the heart and anterior tip of the liver in number of ventral scales, expressed as percentage of total number of ventral scales.

Table 3 Geographic variation of internal characters in *H. lapemoides*.

	Sex	*n*	VB-body	VB-heart	%VB-heart	VB-tail
Andaman	M	28	164–174	73–83	43.5–48.0	31–38
Sea and		*x*±SD	170±2.7	79±2.3	46.7±1.1	34±2.0
Malacca	F	23	171–180	79–86	45.1–49.1	28–38
Str.		*x*±SD	174±2.5	82±1.8	47.0±1.1	31±2.5
India	M	2	165–174	79–82	45.4–49.7	37(*n*=1)
and Sri		*x*±SD	169±6.4	80±2.1	47.5±3.0	
Lanka	F	5	171–182	81–94	45.8–51.7	30–35
		x±SD	176±4.9	85±5.1	48.5±2.3	33±1.9
Persian	M	45	171–188	79–90	45.6–51.1	33–40
Gulf and		±SD	177±3.3	85±2.3	47.9±1.3	37±1.7
Gulf of	F	26	172–186	81–90	46.6–49.2	30–36
Oman		*x*±SD	181±3.6	86±2.4	48.0±0.8	34±1.7

VB-body = number of body vertebrae. VB-heart = position of the tip of the heart in relation to the number of vertebrae. %VB-heart = relative position of tip of the heart in number of vertebrae, expressed as percentage of total number of vertebrae. VB-tail = number of tail vertebrae.

1985; Rasmussen, 1987, 1989, 1992; Smith, 1926, 1930, 1943; Taylor, 1965; Toriba & Sawai, 1981; Tweedie, 1983).

The sympatric species differ from *H. lapemoides* in the following characters: *H. cyanocinctus* and *H. spiralis* have the sphenoid nearly excluded from the ventral margin of the optic fenestra (McDowell, 1972; Rasmussen, 1992: Fig. 5), a lesser number (< 9) of maxillary teeth, (< 20) pterygoid teeth, and (< 20) dentary teeth, and a different colour pattern (Bussarawit et al., 1989; McDowell, 1972; Rasmussen, in press; Smith, 1926). *H. brookii*, *H. cantoris*, *H. fasciatus*, *H. gracilis*, *H. klossi*, *H. melanosoma*, and *H. obscurus* have a triangular flange on the palatine (McDowell, 1972; Rasmussen, 1992: Fig. 4), and a lesser number (< 8) of maxillary teeth, (< 17) pterygoid teeth, and (< 16) dentary teeth (McDowell, 1972). *H. bituberculatus* has a lesser number (25-29) of scale rows around neck, a lesser number (247-290) of ventrals, a lower position (90-105 VS) of heart tip, and a different colour pattern (Rasmussen, 1992). *H. caerulescens* has a higher number (14-18) of maxillary teeth (Smith, 1926), a higher position (96-99 VB, based on 3 specimens from Phuket harbour) of heart tip, and a different colour pattern (Bussarawit et al., 1989; Smith, 1926; Tweddie, 1983). *H. inornatus* (type specimen BMNH 1946,1.1.27 formerly III.7.1.a.) has a lesser number (253) of ventrals, a lower position (86 VS) of heart tip, a lower position (67 VB) of heart tip, and a different colour pattern (Rasmussen, 1989). *H. lamberti* is compared with *H. lapemoides* in the section concerning species assignment. *H. mamillaris* has a smaller head, a lesser number (25-29, 35-43) of scale rows on neck and body, and a different colour pattern (Minton, 1966; Smith, 1943). *H. ornatus* has a lesser number (224-294) of ventrals, a lower position (72-104 VS) of heart tip, a lower position (59-65 VB) of heart tip, and a different colour pattern (Rasmussen, 1989). *H. stricticollis* has a smaller head, a higher number (> 200 VB, Voris, 1975, and own observation) of vertebrae, and the hemipenis is bilobed half way down. *H. torquatus* has a higher position (91-105 VB) of heart tip, and a lesser number (7-8) of maxillary teeth (only in Malacca strait) (own observation).

Comparison with allopatric species

In the genus *Hydrophis* the following species are allopatric with *H. lapemoides*: *H. belcheri*, *H. coggeri*, *H. czeblukovi*, *H. elegans*, *H. geometricus*, *H. macdowelli*, *H. melanocephalus*, *H. pacificus*, *H. parviceps*, and *H. vorisi*. (Bussarawit et al., 1989; Cogger, 1975; Kharin, 1983, 1984a, 1984b; McCarthy & Warrell, 1991; Smith, 1986; Smith, 1926, 1930, 1935). The allopatric species differ from *H. lapemoides* in the following characters: *H. coggeri*, *H. czeblukovi*, *H. elegans*, *H. melanocephalus*, and *H. pacificus* have the sphenoid nearly excluded from the ventral margin of the optic fenestra (Kharin, 1984b; McDowell, 1972; Rasmussen, 1992: Fig. 5) and a lesser number (< 9) of maxillary teeth, (< 20) pterygoid teeth, and (< 20) dentary teeth (Kharin, 1984b; McDowell, 1972). *H. parviceps* and *H. vorisi* have a triangular flange on the palatine (Kharin, 1984a; McDowell, 1972; Rasmussen, 1992: Fig. 4), and a lesser number (< 8) of maxillary teeth, (< 17) pterygoid teeth, and (< 17) dentary teeth (Kharin, 1984a; McDowell, 1972; Smith, 1935). *H. belcheri* has a lesser number (24-26, 32-36) of scale rows on neck and body, a lesser number (14-17) of pterygoid teeth, and no cuneate scales at infralabials (McCarthy & Warrell, 1991). *H. geometricus* has a high number (51-58, a small overlap) of scale rows on body, and a different colour pattern (Smith, 1986:152 Fig. 1). *H. macdowelli* has a lesser number (< 8) of maxillary teeth, (< 16) pterygoid teeth, and (< 17) dentary teeth, and a lesser number (256-266) of ventrals (Kharin, 1983).

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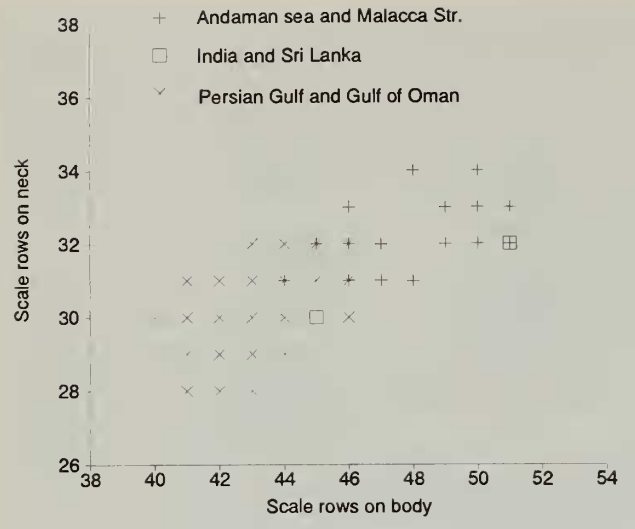

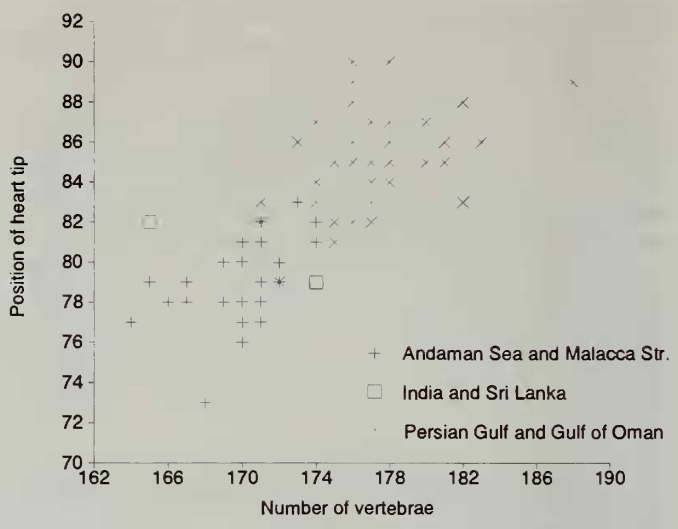

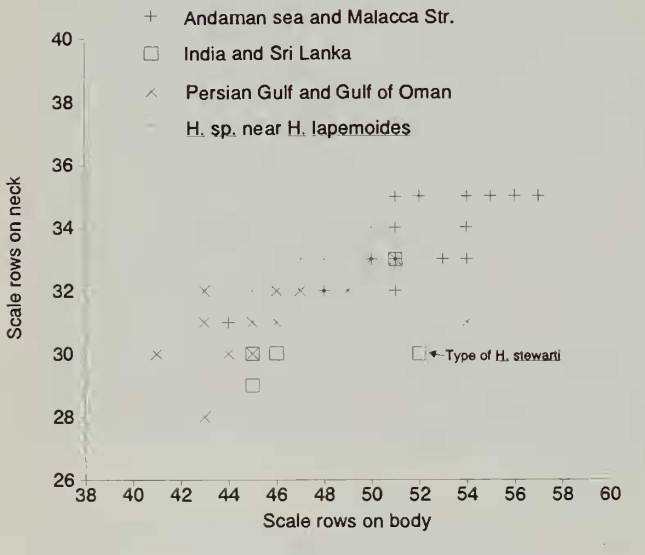

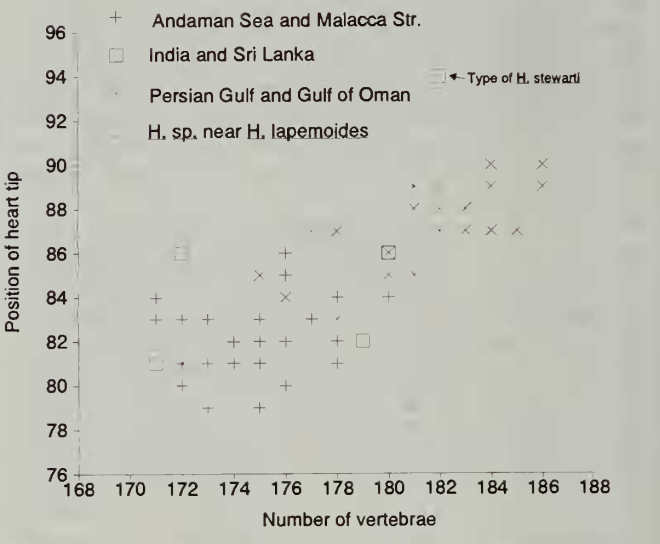

Fig. 6 Relation between number of scale rows on body and number of scale rows on neck in males (top) and females (bottom) of *H. lapemoides*, showing geographic variation.

Fig. 7 Relation between number of body vertebrae and position of heart tip in males (top) and females (bottom) of *H. lapemoides*, showing geographic variation.

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